

BREEDING ECOLOGY OF THE PUAIOHI (*MYADESTES PALMERI*)

THOMAS J. SNETSINGER,^{1,2,3,6} CHRISTINA M. HERRMANN,^{1,2,3}
DAWN E. HOLMES,^{1,4} CHRISTOPHER D. HAYWARD,^{1,4} AND
STEVEN G. FANCY^{1,5}

ABSTRACT.—We studied the breeding ecology of the critically endangered Puaiohi (*Myadestes palmeri*), a poorly known Hawaiian thrush endemic to the island of Kauai. From 1996 through 1998, we monitored 96 active nests over the course of three breeding seasons. Mean clutch size was 2.0, and pairs produced an average of 1.5 fledglings/successful nest. Pairs renested after failure and some raised multiple broods. The mean annual reproductive effort was 2.1 nesting attempts/territory, and pairs produced a mean 1.1 fledglings/attempt. Large differences in nesting effort and productivity occurred among years, with mean number of fledglings/territory ranging from 0.4 to 4.9. Predation by owls (probably Short-eared Owls, *Asio flammeus*) and introduced rats (probably black rats, *Rattus rattus*) accounted for most nest failures. The presence of non-breeding floaters in the population and their largely unsuccessful attempts to gain territories in the study area suggest that the population is near carrying capacity. The high reproductive potential of the Puaiohi may help explain its persistence despite the species' historical rarity. Received 29 April 2004, accepted 22 November 2004.

The Puaiohi (*Myadestes palmeri*) is a rare and poorly known thrush restricted to forests above 1,000 m elevation on the island of Kauai in the Hawaiian Islands. Of the five Hawaiian thrushes, it is the most divergent vocally, morphologically, and behaviorally (Pratt 1982). Except for the Omao (*M. obscurus*) on the island of Hawaii, the other species are considered critically endangered or extinct (Collar et al. 1994, Reynolds and Snetsinger 2001).

Intensive efforts over the last 4 decades to document the status of Hawaii's forest birds suggested that the Puaiohi was exceedingly rare and had experienced a range contraction since the 1960s (Sincock et al. 1984, Scott et al. 1986, Pyle 1994). In the course of these studies, a number of factors were implicated in the loss of Hawaii's forest bird populations. It is thought that habitat modification, avian disease, competition, and predation have acted in concert to diminish available habitat and

reduce survival and reproduction. Surveys conducted by the U.S. Fish and Wildlife Service (USFWS) and Hawaii Department of Land and Natural Resources (DLNR) in 1993 and 1994 suggested that the Puaiohi was on the brink of extinction (USFWS, DLNR unpubl. data).

Published descriptions of three known Puaiohi nests suggest that the Puaiohi usually nests on cliffs along streambeds (Kepler and Kepler 1983, Ashman et al. 1984, Harrity et al. 1995). These descriptions, along with a few incidental observations and a sparse record of published anecdotal information (Perkins 1903, Richardson and Bowles 1964), were all that was known of the breeding biology and life history of the Puaiohi. The discovery in April 1995 of a fledgling Puaiohi and at least three breeding pairs on the Alakai Plateau of Kauai, near the Koaie Stream Gauging Station (Harrity et al. 1995), prompted a 3-year interagency study. The goals of the study were to determine the status of the population, collect life-history information, assess limiting factors, and develop and evaluate management strategies to promote the protection and expansion of this species into appropriate habitat within its historical range. Concurrently, the Zoological Society of San Diego (ZSSD) and U.S. Geological Survey (USGS) developed captive propagation and release techniques for the closely related Omao to assist in expanding the range of the Hawaiian *Myadestes* (Kuehler et al. 2000, 2001; Fancy et al. 2001).

¹ U.S. Geological Survey, Pacific Island Ecosystems Research Center, P.O. Box 44, Hawaii National Park, HI 96718, USA.

² Pacific Coop. Studies Unit, Dept. of Botany, Univ. of Hawaii, Honolulu, HI 96822, USA.

³ Current address: 35289 Washburn Heights Dr., Brownsville, OR 97327, USA.

⁴ Current address: 54 Wildflower Dr., Amherst, MA 01002, USA.

⁵ Current address: National Park Service, 1201 Oak Ridge Dr., Ste. 200, Fort Collins, CO 80525-5596, USA.

⁶ Corresponding author; e-mail: puaiohi@peak.org

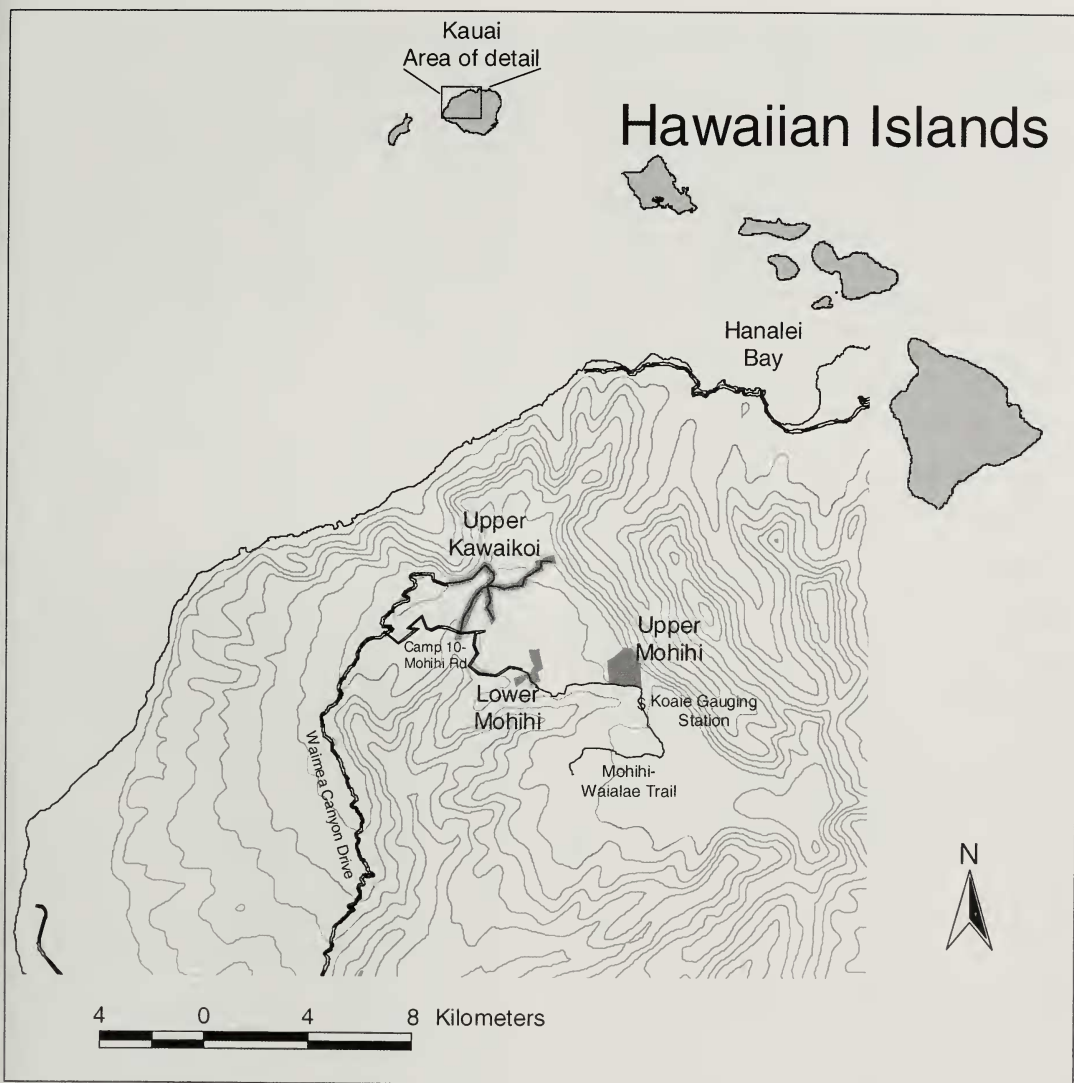


FIG. 1. Upper Mohihi, lower Mohihi, and upper Kawaikoi Puaiohi study areas (shaded) on the island of Kauai (1995–1998). Contours are 150 m apart.

METHODS

Study area.—We established a base camp at the Koaie Gauging Station at the 4.0-mile (6.5 km) marker along the Mohihi-Waialae Trail (Fig. 1) due to its proximity to previously noted Puaiohi breeding activity. During September 1995–January 1996, we conducted preliminary surveys in this area and other areas of suitable habitat. We monitored these areas from 1996 through 1998. Through our initial surveys we located a population concentration at 1,250 m elevation along the upper stretches of the Mohihi Stream and its tributaries, and

we selected a 2-km² study area that included 66 ha along 3.8 km of the Mohihi Stream bottom. We also found several isolated Puaiohi pairs in the neighboring Koaie drainage and monitored their breeding activity as well. Lastly, we selected 4 km of stream bottom on the lower Mohihi Stream (where Puaiohi were rare) and 8 km of stream bottom and trails in the upper Kawaikoi Stream drainage (where Puaiohi were not detected) to conduct Puaiohi surveys and habitat-related research.

The vegetation at each of the three study areas (upper Mohihi and territories in the ad-

jacent Koaie drainage, lower Mohihi, and upper Kawaikoi) was dominated by a dense ohia (*Metrosideros polymorpha*) canopy. A wide variety of other trees and shrubs made the forest structurally diverse with a dense, well-developed understory. The rainy season extended from November through March and was wet but variable, with an average daily rainfall of 19.2 mm/day for 1995–1996 and 1996–1997. The mean daily rainfall for the same period in 1997–1998 was just 6.5 mm/day. The upper Mohihi differed from both the lower Mohihi and upper Kawaikoi in having narrower, steeper drainages with more vertical cliff walls.

Nest monitoring.—We searched for nests at known activity centers at least once every 3 days from the onset of breeding in March through the end of breeding in September (August in 1998). Weather permitting, we checked nests every other day and recorded the status: inactive (under construction, fledged, failed, or in latency—the lag between nest completion and the first egg), laying, incubating, hatching, nestling, or unknown. We counted nestlings and/or eggs when this could be done without undue disturbance to the nest. Using a combination of clues, we attempted to determine the cause of nest failures. We attributed predation to owls if the nest was completely removed and if we had observed owl activity nearby prior to predation. If we found partially eaten remains of young or adults or the presence of rat feces in the nest, we concluded that rat predation was the cause of nest failure. For each year we report the mean \pm SD for the various stages of nesting and the length of the breeding season (annual period from mean first egg laid date through mean final nest failure or fledge date), which was determined for pairs in which all breeding activity was documented within a year.

Every 1–3 days we monitored selected ($n = 43$) nests for 1–4 hr during all stages of nesting to determine nest attendance rates and nestling food requirements. We monitored activity with a spotting scope or binoculars from a blind (15–50 m from the nest) or, if blind placement was not possible, from a sufficient distance so as not to influence normal behavior. Observers recorded all nest activity (sex and age of the attending bird, behavior, time, and weather conditions) by dictating into a

micro-cassette recorder. When a bird was not identifiable by the presence of a unique breast pattern of retained juvenile feathers or color bands, age was determined by the presence or absence of retained juvenile scalloping. Sex of unknown birds was determined by behavior (brooding and incubating were associated only with females in this study), evidence of a brood patch (females; Ashman et al. 1984, this study), or the concurrent observation of the bird's known-sex mate (e.g., the male was singing from a perch near the nest; only males sang in this study) and no evidence of helper activity at the nest. Additionally, in 1997, while adults were absent from nests, we measured and described eggs ($n = 29$) and color-banded, weighed, and measured nestlings ($n = 20$).

We found nearly all Puaiohi nests on shelves or in cavities of streamside cliff walls. Once nests were no longer active, we recorded wall height at the nest, nest height on the wall, cavity or shelf dimensions (maximum depth, height, width), concealment (single ground-based visual estimate of how obscured [%] the nest was from a distance of 5 m from the nest), wall vegetation, distance to flowing stream, and direction of exposure. We recorded nest material for nests in fresh condition and took the following nest measurements: overall height, depth of cup, width of rim, and diameter of cup. Nest characteristics are reported as means \pm SD. Sample sizes varied for some characteristics, as nest and cavity measurements required close inspection of the nest site and many nests were too high to allow for this. In other cases we failed to collect complete information.

Territory size and spacing.—The rugged terrain made it impossible to follow individual Puaiohi and map territory boundaries. However, we were able to map locations of nests and sightings of color-banded birds using compass bearings and measured distances from known points on a 1:1,000 scale map of the study area. Using plotted positions for active nests, we measured the straight-line distance to the nearest neighbor's active nest, and report the mean of this value as a measure of nest density. When an active nest was surrounded by neighboring territories that were occupied by non-nesting Puaiohi, we recorded no value.

Management intervention.—We removed eggs from some nests for captive propagation and poisoned rats in the vicinity of active nests to reduce rodent predation. Eggs were taken from one inactive and six active nests over the course of the study (seven eggs from three nests in 1996 and eight eggs from four nests in 1997). We distributed four tamper-resistant bait stations containing 227 g each of Eaton's Bait Block Rodenticide (contains 0.005% diphacinone) evenly on the ground below nests ($n = 27$) and 5–20 m from the base of the nest cliff. Bait stations were placed only around nests that were found at least 1 week before fledging. Rats must repeatedly ingest the diphacinone bait over approximately 7 days for the bait to be effective, and recent fledglings often perch low in bushes or on the ground for a few days after leaving the nest, making them susceptible to rat predation. We checked and replaced bait weekly according to label instructions. Because protecting nests of this species was a high priority, nests were not randomly selected for bait treatment. We did not treat nests discovered within 7 days of fledging, those >20 m high, those where terrain did not allow access to the base of the nest wall, and those discovered when personnel were insufficient to maintain the bait stations.

We tested for independence of nest fate for nests that were and were not protected by rat poisoning using a chi-square test (Statistix for Windows 2.0, $\alpha = 0.05$). Nest fate was categorized as failed (four categories) or fledged. The four failure categories were rat predation, owl or unknown predation, non-predation failure, and unknown.

We attempted to minimize the effects of our interventions on our data. We did not use data on nests from which eggs were removed for captive propagation in the calculation of breeding season length or fecundity statistics. In determining nest survival rates (see below), we used data only from unprotected nests. As most of the nests from which eggs were removed for captive propagation were in the middle of our study area, the effect of these artificial failures could have had unknown effects on neighboring territories. Similarly, rat control at nests may have influenced rat populations at neighboring nests where there was no rat control. Both effects are likely negli-

gible, given the Puaiohi's propensity to rapidly renest following nest failure and the relatively large nearest-neighbor distances between active nests.

Reproductive effort and success.—We used Mayfield's (1961, 1975) method to determine daily and overall survival rates for the incubation ($n = 633$ egg-days [43 nests]), hatch ($n = 90$ eggs [45 nests]), and nestling ($n = 715.5$ nestling-days [41 nests]) stages for nests in the upper Mohihi study area that were not protected against rats. When nests fledged or failed between visits, fate was assigned to the midpoint between observations. We present 3-year daily survival rates for the incubation and nestling periods as mean \pm SE. Because we were uncertain of hatching period length, we treated hatching as either successful or unsuccessful and report hatching survival simply as percent eggs hatched. We calculated egg-to-fledging survival as the product of survival probabilities (incubation, hatch, and nestling).

We documented the season-long reproductive success for 48 territories over the 3 years of our study. A few individuals ($n = 6$ birds at 12 territories) were color marked, and we could occasionally identify individuals ($n = 13$ birds at 11 territories) through the presence of unique residual scalloping on the breast feathers in second-year (SY) birds. No color-banded individuals were observed actively breeding until 1997.

We report measures of reproductive success per territory (rather than per female). To count the number of young fledged, we visited all nests within 3 days of the fledge date and again ≤ 1 week later. Accurate counts were possible because (1) parents fed new fledglings often, (2) new fledglings were poor fliers, (3) they remained perched in low shrubs <50 m from the nest during the first few days after fledging, and (4) they typically stayed within 100 m of the nest during the next few weeks. We used the maximum count of observed young fledged to calculate fecundity statistics. We report annual means and 3-year means \pm SD for fledglings/territory, young fledged/successful nest, nesting attempts/territory, and fledglings/attempt. We compared fledging dates of one- and two-chick nests using ANOVA, and we compared the time from nest completion (for successful versus failed

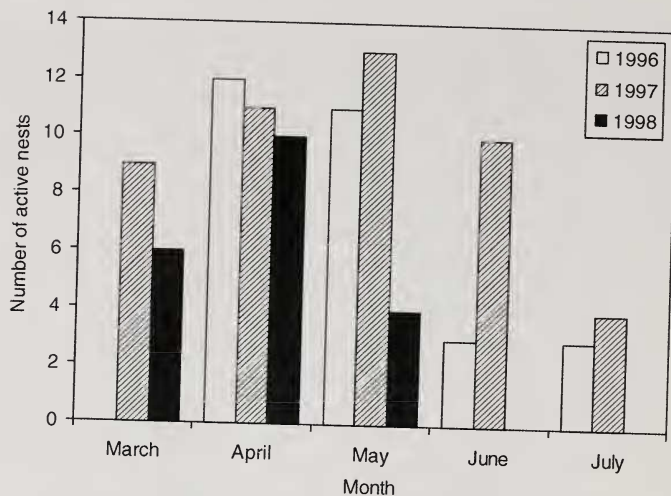


FIG. 2. Number of active Puaiohi nests ($n = 96$) by month according to first egg date. We back-dated for nests found after this date ($n = 56$), assuming a 13.5-day incubation period and 18.3-day nestling period (this study). Some March and April nests may have been missed in 1996 due to a lack of observer familiarity with the study area.

nests) until the onset of renesting with a t -test (Statistix for Windows 2.0, $\alpha = 0.05$).

Survival.—As time allowed, we trapped, banded, and color marked Puaiohi using mist nets set up in the vicinity of active nests or along ridgetops where Puaiohi were regularly observed. Sample sizes were too small to use capture-recapture modeling to estimate survival, and we report minimum annual survival based on resightings for two age categories (HY, AHY) from one breeding year to the next, using April as the start of the breeding season.

RESULTS

The Puaiohi breeding season began in March–April and usually ended in August, although in one year it continued into September. We found no active nests after August, but a recently fledged juvenile was observed in late September, indicating nesting can continue into that month. Breeding season lengths were 87 days (1996), 132 days (1997), and 51 days (1998).

The complete nesting cycle took 46 days: nest construction lasted 2.9 ± 2.0 days (range = 1–7 days, $n = 15$), the latency period was 9 ± 0.6 days (range = 8–10 days, $n = 12$), incubation lasted 13.5 ± 0.6 days (range = 13–14 days, $n = 4$), and the nestling period was 18.3 ± 1.7 days (range = 16–22 days, n

= 13). Eggs were laid one/day. Incubation began with clutch completion and hatching was synchronous (<24 hr) within broods.

Territory occupation and nest density.—We found 112 nests, 96 of which were active (Fig. 2). The active nests were distributed over the 3 years as follows: 1996—29 nests (representing a complete reproductive effort in 12 territories plus a partial effort in 8 territories); 1997—47 nests (representing complete reproductive effort in 14 territories plus partial effort in 10 territories); 1998—20 nests (representing complete reproductive effort in 22 territories plus partial effort in 4 territories). The remaining nests either were not used or were found after use and were distributed over the period of the study as follows: 4 nests (1996), 10 nests (1997), 2 nests (1998). In addition, we found 97 Puaiohi nests that had been constructed and possibly used in a year prior to their discovery.

Puaiohi pairs were distributed at approximately 150-m intervals along 3.8 km of the Mohihi Stream. Mean straight-line distance between active nests was 86 ± 17 m (range = 59–119 m) in 1996, 79 ± 14 m (range = 58–103 m) in 1997, and 133 ± 40 m (range = 98–204 m) in 1998. Twenty-four territories were occupied by territorial pairs within the accessible portion of our study area throughout the study. The density of territorial Pu-

TABLE 1. Puaiohi nest and nest-site characteristics, Mohihi drainage, Alakai Swamp, Kauai, 1996–1998.

	<i>n</i>	Mean	SD	Maximum	Minimum
Height of wall (m)	157	9.5	4.8	35	3
Height above ground (m)	172	4.2	2.6	16	0.6
Distance from stream (m)	151	7.6	9.7	40	0
Width of nest cavity (cm)	46	39.4	23.4	90	7
Height of nest cavity (cm)	46	26.9	13.2	70	10
Depth of nest cavity (cm)	38	21.4	10.8	50	0
Nest concealment (%)	153	69	31.2	100	0
Outer diameter of nest (cm)	33	14.3	2.7	21	10
Inner diameter of nest (cm)	27	8.0	1.3	10	6
Height of nest (cm)	31	8.1	3.5	14	2
Nest-cup depth (cm)	27	5.4	1.5	8.7	3
Nest-rim thickness (cm)	29	3.2	0.7	4.5	2
Direction of exposure (°)	144	161	106	338	0

aiohi in the Mohihi study area was 6.3 pairs/km of primary stream bottom. The additional length of feeder streams that were too short to support more than a single territory were not included in the calculation of primary stream bottom. Non-territorial, single birds were also observed throughout the study area; however, because many of these birds were unbanded and could not be sexed accurately, we could not determine the size or structure of this population. Individual birds within a territory were occasionally replaced, but only one new territory was established in 3 years. When uniquely plumaged ($n = 13$) or color-banded ($n = 6$) individuals held territories, we observed only one case of turnover of a bird within a breeding season. All banded birds (two adult males and one adult female) that we monitored on breeding territories in 1997 returned to defend the same territory in the 1998 breeding season.

At least 10.0% of territories had SY females and $\geq 6.7\%$ had SY males ($n = 60$ pair-years). At 8.0% of 87 nests, we noted some form of helper activity in which non-breeding Puaiohi helped in the defense and maintenance of nests and/or feeding of young. These birds were fledglings from previous clutches of the same pair ($n = 2$) or SY non-breeding birds with an unknown relationship to the breeding adults ($n = 5$); in one case, the SY helper was known not to be related to either breeding adult.

Nest sites, nests, and eggs.—Most nests were constructed in cavities or on shelves of streamside cliff faces. Only 5% of active nests

($n = 93$) were in other locations: four were in secondary cavities in dead ohia snags, and one was in a crevice along the side of fallen log that bridged a small stream. One inactive nest was found in the trunk of a hapuu (*Cibotium* sp.) tree fern.

Nest sites ranged from true cavities, in which the nest was completely concealed and accessed through a small hole in the cliff wall, to exposed flat shelves with little protective cover (Table 1). The majority of nests were positioned on flat shelves partially concealed from above by a protective “umbrella” of ferns and a slight overhang of the cliff nest wall. While two nest walls were dry and covered with only a light growth of lichen, 97% ($n = 77$) were damp and covered with a verdant growth of small, native plants: native ferns (predominantly *Sadleria squarrosa*), liverworts, and scattered small shrubs and trees (e.g., olapa and lapalapa, *Cheirodendron* spp.; *Cyanea hirtella*; kanawao, *Broussaia arguta*; pukiawe, *Styphelia tameiameia*; and ohelo, *Vaccinium* spp.).

Nests ($n = 110$) were open-cupped with an outer matrix composed of mounded native mosses, uluhe (false staghorn fern, *Dicranopteris linearis*), liverworts, other bryophytes, painiu (a native lily, *Astelia* spp.) and sedge (*Carex* spp.) leaves, clubmosses (*Lycopodium* spp.), other ferns, grasses, and ohia rootlets. The cup lining was woven of pulu (a soft hair-like substance from hapuu), moss sporophytes, shredded grasses and sedges, or painiu leaves. Usually, an untidy mass of nesting material formed a tail, up to 20 cm long, extend-

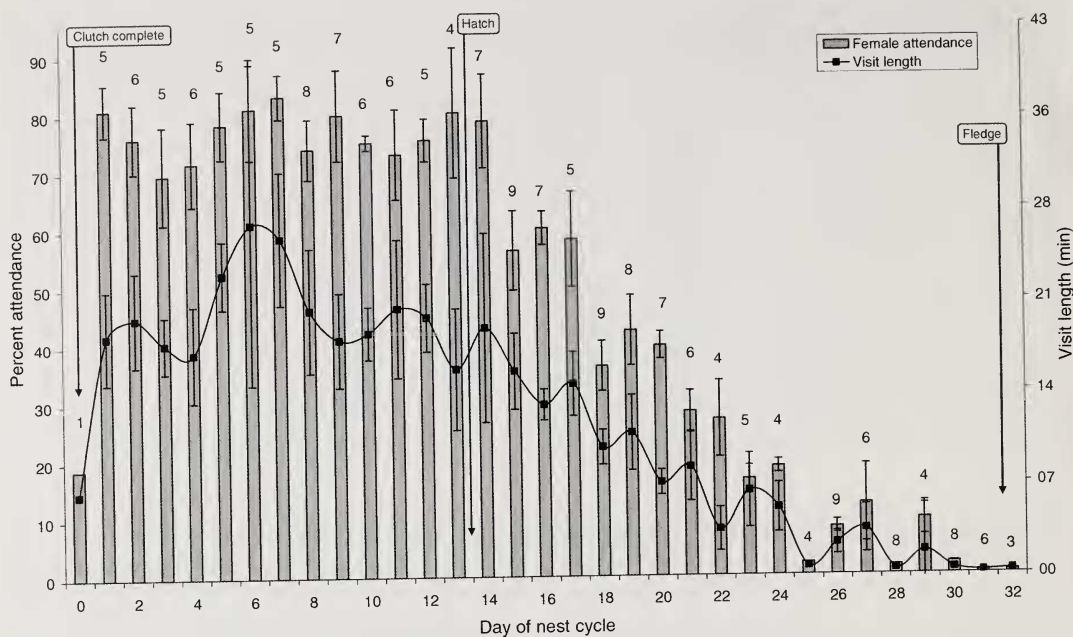


FIG. 3. Female Puaiohi nest attendance and nest-visit duration. Numbers of nests monitored are shown above bars. Error bars are \pm SE.

ing out of the cavity mouth or off the shelf ledge from the base of the nest.

All clutches consisted of 2 eggs ($n = 39$). Eggs had a smooth surface and their shape varied from sub-elliptical to ovoid. Eggs ($n = 29$) measured 24.77 ± 1.70 mm (range = 22.11–29.80 mm) \times 18.18 ± 1.23 mm (range = 15.75–21.16 mm), and eggshell thickness ($n = 3$) was 0.14 ± 0.02 mm (range = 0.12–0.16 mm).

Background color of eggs varied, sometimes within a clutch, from a very pale greenish-blue at the light end of the spectrum to brownish-mauve at the dark end. All eggs had irregular rust, brown, mauve, and tan splotches and black and brown scrawls scattered over the surface, but concentrated at the blunt end.

Nesting through fledgling observations.—During incubation, the male was responsible for territory defense; after hatching, he fed the female and young. Incubation and brooding were performed solely by the female, but both adults shared provisioning and maintenance duties (females responsible for 56% of the nest visits, males 9%, and undetermined parent or helper 35%; $n = 848$ nest visits in 461 hr of observation at 42 nests). During the nestling period, female visitation rates were $2.8 \pm$

0.2 visits/hr. Males made 0.68 ± 0.08 visits/hr during the same period.

Overall nest attendance was fairly high during incubation and then gradually dropped off as brooding proceeded (Fig. 3). Female nest attendance was $81 \pm 4\%$ SE ($n = 5$) a day after clutch completion and averaged 77% ($n = 73$) during the incubation period. One day after hatch female attendance dropped to $56 \pm 7\%$ SE ($n = 9$).

Over the entire nesting period, the relative frequencies of provisioning nestlings with invertebrates and fruit were nearly equal; however, young were fed invertebrate prey exclusively until 6 days of age, when fruit was first incorporated into the nestling diet. Nestlings received fruit during 48% of the feedings in which the food item was observed ($n = 79$). In order of decreasing frequency, these fruits were olapa/lapalapa, painiu, kanawao, ohelo, and “thimbleberry” (West Indian raspberry, *Rubus rosifolius*). Invertebrates were fed to nestlings 51% of the time. In order of decreasing frequency, these were moths, damselflies, earthworms, caterpillars, dragonflies, spiders, beetle larvae, and beetles. On one occasion we observed a nestling being fed a skink.

Young in one-chick nests ($n = 4$ nests) had

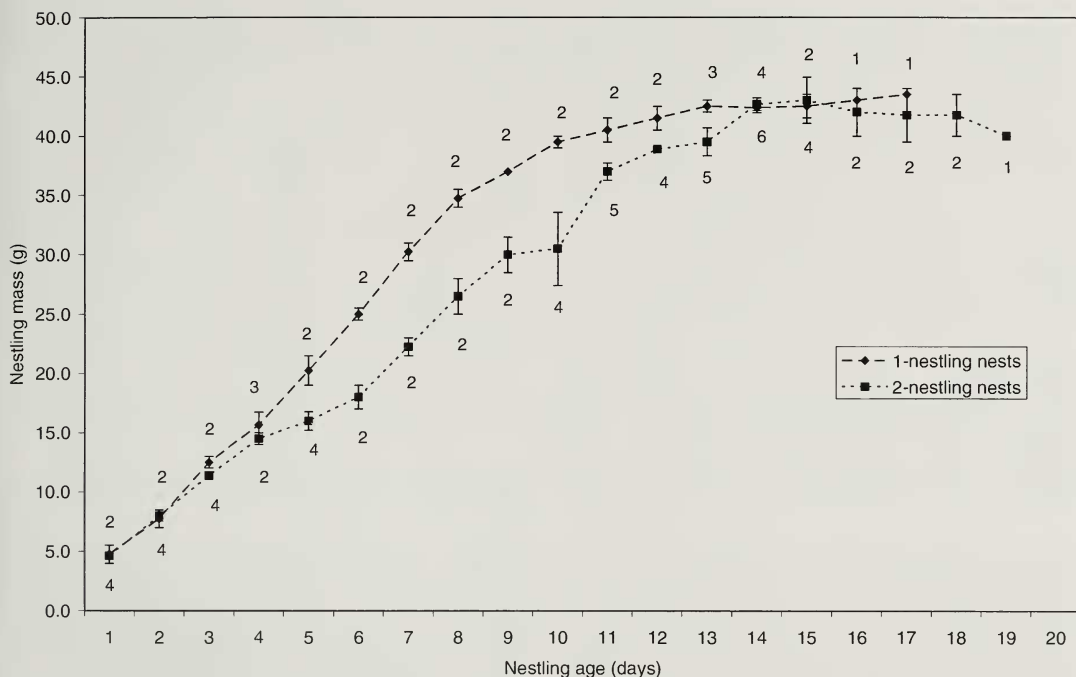


FIG. 4. Puaiohi nestling growth curves (mean mass, standard error bars). Number of nestlings weighed are shown above (1-nestling nests, $n = 4$) or below (2-nestling nests, $n = 16$) each point. Young in 1-nestling nests fledged at days 16–19, and, in 2-nestling nests, they fledged at days 16–21.

mean weights that were greater than those of young in two-chick nests ($n = 16$ nests) through early development, but once the chick's growth in one-chick nests began to plateau around nestling day 12, there was little difference in weights (Fig. 4). The nestling period of two-chick (16.3 days) and one-chick (16.6 days) nests did not differ (one-way ANOVA; $F_{1,55} = 0.36$, $P = 0.55$).

After fledging, males were responsible for 81% of the feedings, females accounted for 8%, and an unidentified parent or helper accounted for 11% ($n = 62$ feedings at 10 nests). Fledglings remained dependent on parents for 3–5 weeks after fledging ($n = 73$ nests). During this period no young were observed >100 m from the nest site.

Reproductive effort and success.—Nesting effort and productivity differed among years (Table 2). In 1996 ($n = 12$ territories) and 1997 ($n = 14$ territories), median nesting effort was three nests per territory. In 1998, a relatively poor year, the nesting season was restricted to 4 months ($n = 22$ territories) with a single nesting attempt being the median effort among closely monitored territories. The

interval between nesting attempts was 10.2 ± 4.0 days (range = 5–18 days, $n = 12$ nest-renewal periods with exact dates known) following nesting success or failure. The outcome of the first nest did not affect the time interval between nest attempts ($t_{10} = -0.12$; $P = 0.91$). The most prolific pair fledged seven young from four (of five total) nesting attempts.

Daily probability of survival (3 year mean \pm SE) during the incubation period was 0.949 ± 0.032 ($n = 633$ egg-days [43 nests]) and during the nestling period was 0.980 ± 0.012 ($n = 715.5$ nestling-days [41 nests]). The probability of a fully incubated egg hatching was 0.864 ± 0.052 ($n = 90$ eggs [45 nests]). Egg and nestling survival both showed similar dramatic decreases in the 1998 field season, while the probability that an egg incubated to term would hatch remained near the overall average (Fig. 5). The probability of survival for the egg-to-fledging period was 0.406 ± 0.176 (3-year mean \pm SE).

Of 21 nest failures, we attributed 48% to predation (19% rats [probably black rats, *Rattus rattus*], 10% owls [we suspect the Short-

TABLE 2. Distribution of number of young Puaiohi fledged per territory, by breeding season (all nesting attempts known), and summary of fecundity statistics, upper Mohihi study area, Kauai, 1996–1998.

Number of young fledged	1996	1997	1998	Mean \pm SD (1996–1998)
0	1	0	14	—
1	0	0	7	—
2	2	1	1	—
3	7	0	0	—
4	2	5	0	—
5	0	2	0	—
6	0	5	0	—
7	0	1	0	—
Total territories	12	14	22	16 \pm 5.3
Mean fledglings/territory	2.8	4.9	0.4	2.3 \pm 2.2
Young fledged/successful nest (no. nests)	1.7 (20)	1.9 (37)	1.0 (9)	1.6 \pm 0.4
Nesting attempts/territory (no. attempts)	2.2 (26)	3.3 (44)	1.1 (24)	2.4 \pm 1.4
Fledglings/attempt	1.4	1.7	0.4	1.1 \pm 0.7

earred Owl, *Asio flammeus*, based on our observation of this species near these nests], and 19% unknown), 14% to abandonment, 5% to weather, 5% to disturbance by non-nesting Puaiohi, 5% to hatch failure, and 24% to unknown causes. Puaiohi reused historically successful nest sites. We never observed reuse of a nest site that failed to produce young ($n =$

4 failed nests at territories in which no subsequent nesting attempt was made). We documented reuse (1–3 times) of 18 historically successful nests in 11 different territories.

Dispersal, fidelity, and philopatry.—Five of the 31 nestlings (16%) that we banded in 1997 exhibited territorial behavior within our study area the following year, establishing an area

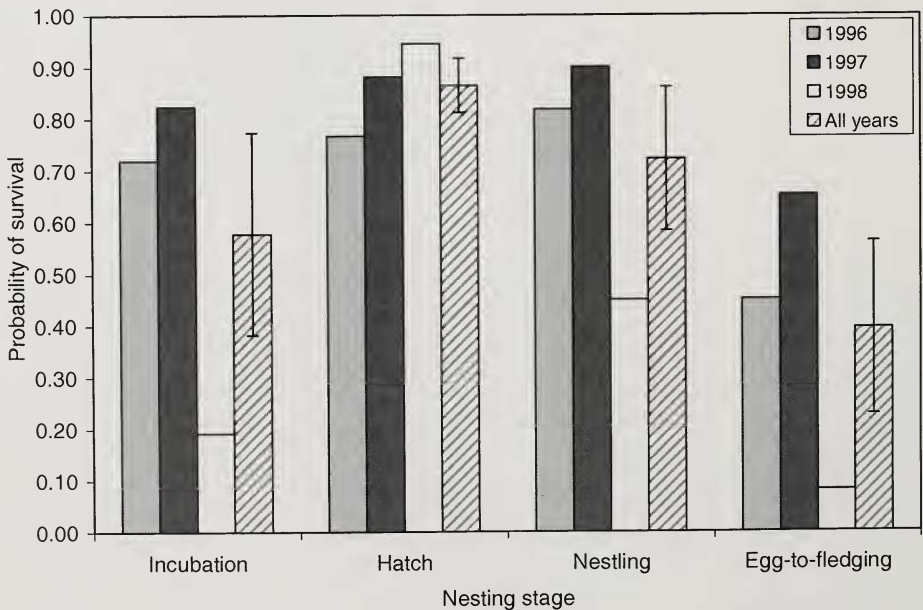


FIG. 5. Egg and nestling survival of Puaiohi for incubation, hatch, nestling, and egg-to-fledging stages by year and all years combined for nests without rat protection ($n = 633$ egg-days [43 nests], $n = 90$ eggs [45 nests], $n = 715.5$ nestling-days [41 nests]). Nesting stage survival values were calculated using Mayfield daily survival rates for the incubation (13.5 days) and nestling stages (18.3 days); hatching survival is simply percent eggs hatched. Egg-to-fledging survival is the product of egg, hatch, and nestling survivals. Error bars are \pm SE.

of activity that was occupied for at least 8 weeks. Distance to natal nest from the activity center was 279 ± 157 m (range = 137–538 m, $n = 5$). One male succeeded in nesting 300 m from its natal site. Two others were observed within 50 m of their natal sites on at least one occasion, and two additional SY birds were documented as floaters >300 m from their natal sites.

Survival.—At least 25% of HY birds survived until April of the year following their banding (7 of 34 unknown sex and 2 of 2 males), and 73% of AHY Puaiohi survived until the following April (2 of 5 unknown sex, 2 of 2 females, and 4 of 4 males).

Predators and predator control efforts.—We protected 27 nests during 576 nest-days with rat bait stations. We monitored an additional 54 untreated nests over 1,038 nest-days. Nest fate and nest protection with rat poison were not independent ($\chi^2 = 11.62$, $df = 4$, $P = 0.020$). At protected nests, rat predation was 0%, owl or unknown predation was 3.7%, non-predation failure was 0%, unknown failure was 0%, and 96.3% fledged ≥ 1 young. At unprotected nests, rat predation was 7.4%, owl or unknown predation was 13.0%, non-predation failure was 16.7%, unknown failure was 1.9%, and 61.1% fledged ≥ 1 young. Nest failures confirmed to have been caused by rat predation increased from 0% in 1996 and 1997 to 36% ($n = 11$ failures) in 1998, when eggs, nestlings, and an incubating female Puaiohi were depredated by rats. However, 8% of nests in 1996 and 3% of nests in 1997 failed due to unknown causes, at least a portion of which may have been caused by rat predation. There was no evidence of rat predation at any of the nests with rat bait stations.

DISCUSSION

The Puaiohi is a species on the brink of extinction, but it is not too late for constructive, affordable management action. It is not so rare that researchers ponder whether or not it is extinct or debate the pros and cons of removing the population from the wild. However, the situation is dire enough to cause alarm and draw the attention of managers and researchers. The Puaiohi population numbers in the hundreds, not in the thousands, and even over the few square kilometers where we found its population to be the most dense, the

Puaiohi was uncommon or rare. Predation by rats is the one clear threat that our research documented, but others loom in the background. Habitat modification through the establishment of invasive plant species and increasing exposure to avian disease both rank as serious future threats.

Through our limited surveys in three study areas, we found the Puaiohi was rare or absent over large areas of apparently suitable habitat. Expansion of the Puaiohi's current range to include all available habitat and efforts to increase the Puaiohi's density in sparsely occupied areas should rank high among efforts to manage this species' recovery. Long-term efforts to slow the establishment of invasive weeds in the Alakai and to develop techniques to eradicate or reduce rat populations there are both important to the survival of the Puaiohi. Cultivating the political will to put these steps into action is just as crucial, and without this support no rat control will ever occur in the wild, where it is needed. If all of these efforts can be implemented, they will undoubtedly have ancillary benefits in promoting the survival of other endemic species.

While researchers have focused much attention on the role of humans in the extinction or near extinction of much of Hawaii's avifauna, Kauai offers a striking example of the effect of natural events on vulnerable avian populations. Hurricanes Dot (1959), Iwa (1982), and Iniki (1992) each caused serious damage on Kauai and likely negatively affected avian populations. Notably, following Hurricane Iwa, observers documented only a few sightings of four of Kauai's five rarest species: Kamao (*Myadestes myadestinus*), Kauai Oo (*Moho braccatus*), Ou (*Psittirostra psittacea*), Nukupuu (*Hemignathus lucidus*), and Puaiohi. None except Puaiohi has been seen since Iniki.

The Puaiohi was apparently rarer than the Kamao or Ou from its discovery through the 1970s, but today it survives in numbers that appear to rival those of the past; the other species may be extinct (Perkins 1903, Richardson and Bowles 1964, Banko 1980, Sincock et al. 1984, Scott et al. 1986, Conant et al. 1998, Snetsinger et al. 1999, Reynolds and Snetsinger 2001). While life history information on Kauai's other endangered endemics is very limited (Snetsinger et al. 1998, Wakelee and

Fancy 1999, Sykes et al. 2000, Pratt et al. 2001), our data indicate that Puaiohi can be prolific breeders in comparison with Omao (Wakelee and Fancy 1999) and other Hawaiian endemics. Their high fecundity may have been one key difference between the Puaiohi and Kauai's other endangered forest birds and may help to explain their survival.

Population structure and distribution.—Our surveys of the upper Mohihi study area indicated that there was a steady-state breeding population for the entire period of August 1995–August 1998. In 1998, a poor breeding year overall, we noted the establishment of one new territory. In all years we noted the presence of non-breeding floaters, which acted as helpers or made unsuccessful attempts to establish territories. This indicated that the population within the study area was saturated by the end of the 1995 breeding season. Kauai was hit by Hurricane Iniki in September 1992, and USFWS/DLNR surveys in early 1993 showed no indication of Puaiohi breeding and documented only a single individual. This suggests that, at best, 1993 was a poor breeding year. Therefore, Puaiohi either survived in good numbers through Hurricane Iniki, or within two breeding seasons (1994 and 1995) the species recovered enough to saturate the upper Mohihi study area with a full complement of breeding pairs and a detectable floater population.

While our data set was small, our resightings of color-banded birds suggest young Puaiohi exhibit relatively strong philopatry and protracted juvenile dispersal. It is likely that these factors contribute to the establishment of a buffer population of non-breeders and helpers. As first documented by Ashman et al. (1984), we observed no obvious aggression by parents toward older fledglings. In fact, some fledglings assisted in raising subsequent clutches within the same year and were observed near natal territories between years. Adults also showed strong nest-site fidelity within and between years. Strong philopatry and adult nest-site fidelity combined with protracted juvenile dispersal support the theory that Puaiohi dispersal is a slow process.

Among Hawaiian forest bird species, the existence of floater populations is suspected in Omao (Wakelee and Fancy 1999) and documented in Elepaio (*Chasiempis sandwichen-*

sis; Vanderwerf 1998). Vanderwerf (1998) found larger and older floater populations in high-quality habitat than in marginal habitat or in populations with high mortality rates. The Puaiohi populations in the upper and lower Mohihi appear to offer the same contrast, with a well-developed floater population in the upper Mohihi and no detectable floater population in the lower Mohihi study area. While the upper Mohihi's floater population may serve as a buffer to the breeding population, the sedentary nature of these birds also prolongs the process of recovery and recolonization in areas that hold few or no Puaiohi, such as the lower Mohihi. Expansion into these areas is likely to be incremental, as only breeding birds on the periphery of a high-density area would be major contributors to range expansion, when young from their nests disperse into unsaturated habitat.

Translocation of captive-reared birds may be the most effective technique for rapidly expanding the range of this species since captive-reared birds should not demonstrate strong site fidelity—a trait that has proved to be a challenge in some translocation efforts (Fancy et al. 1997). Preliminary translocation efforts have met with mixed success (Kuehler et al. 2000, 2001; Tweed et al. 2003).

Limiting factors affecting breeding.—The Puaiohi's specific nest-site requirements are probably the most important limiting factor within the upper Mohihi study area. This is also probably the case at the lower Mohihi area, but the extremely low Puaiohi density there suggests that other limiting factors may also play an important role.

Most nests were constructed in cavities or on shelves in streamside cliff faces, as described by earlier researchers (Kepler and Kepler 1983, Ashman et al. 1984). Kepler and Kepler (1983) suggested that Puaiohi nest-site selection could make them less susceptible to weather effects. Our results support this conclusion as we noted only one nesting failure that we attributed to weather, despite a number of severe storms during breeding seasons.

Parents provided nestlings with equal proportions of invertebrate prey and mature fruit, suggesting a dependence on both. Lower rainfall in the winter (rainy) season of 1997–1998 may have resulted in low food availability during the 1998 breeding season. Our anec-

dotal observations suggest a scarcity of mature fruit on the Puaiohi's dominant food plants (particularly olapa; kanawao; and ohia ha, *Syzygium sandwicense*) during that period. Low food availability may have contributed to poorer condition of adults and a lack of food for nestlings in that year, either of which could have contributed to poor nesting effort.

An apparent increase in rat predation contributed to low reproductive success in 1998. While there are many possible explanations for the increase in rat predation, one reasonable theory is that a general scarcity of fruit forced the rats to search more widely for food than usual, exploring cliff walls and opportunistically finding and depredating Puaiohi nests. The combination of increased predation and a poor nesting effort reduced the number of fledglings/territory by more than 80% from that observed during each of the preceding 2 years.

Predator control.—Results of rat control efforts indicated that rats have a significant impact on Puaiohi nests and fledglings. Limited poisoning around active nests resulted in a higher proportion of nests that fledged young. Our discovery in 1998 of the depredation of an incubating female and her two eggs by rats emphasized that rats can impact not only nesting productivity but also the adult breeding population.

Predator control was labor intensive, as performed for this study, and would be cost prohibitive on a large scale. Given the protracted breeding season and difficult working environment, it would be exorbitantly expensive even on smaller area, such as the lower Mo'ohi study area. Large-scale rat control efforts such as those involving aerial distribution of rodenticide have the potential for substantial positive impacts (Veitch and Bell 1990, Armstrong and McLean 1995, Empson and Miskelly 1999), and these techniques are the only viable alternatives for rat control over large areas of Puaiohi habitat. However, in addition to cost and other management considerations (e.g., effects on non-target species, secondary poisoning, and potential water supply contamination), political, cultural, and social factors will need careful consideration before such methods can be attempted, even at experimental levels.

Conclusion.—The Puaiohi has proven itself

a survivor. Its fecundity and adaptability to captive propagation make management techniques, such as the reintroduction of captive-bred birds, potentially powerful tools in expanding the current range of the Puaiohi and increasing population density in areas where their numbers are low. However, research into limiting factors in areas of low population density will be a crucial component in the development of a successful management strategy. Effective and politically acceptable, broad-scale rat control techniques will likely play an important role in future management efforts.

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LITERATURE CITED

- ARMSTRONG, D. P. AND I. G. McLEAN. 1995. New Zealand translocations: theory and practice. *Pacific Conservation Biology* 2:39–54.
- ASHMAN, P. R., P. PYLE, AND J. JEFFREY. 1984. A second nest of the Small Kaua'i Thrush. *'Elepaio* 45:33–34.
- BANKO, W. E. 1980. History of endemic Hawaiian birds. Part 1, population histories—species accounts: forest birds: Hawaiian thrushes. Cooperative National Park Resources Study Unit, University of Hawaii, Honolulu.
- COLLAR, N. J., M. J. CROSBY, AND A. J. SATTERSFIELD. 1994. *Birds to watch 2: the world list of threatened birds*. Birdlife International, Cambridge, United Kingdom.
- CONANT, S., H. D. PRATT, AND R. J. SHALLENBERGER. 1998. Reflections on a 1975 expedition to the lost world of the Alaka'i and other notes on the natural

- history, systematics, and conservation of Kaua'i birds. *Wilson Bulletin* 110:1–22.
- EMPSON, R. A. AND C. M. MISKELLY. 1999. The risks, costs and benefits of using brodifacoum to eradicate rats from Kaptiti Island, New Zealand. *New Zealand Journal of Ecology* 23:241–254.
- FANCY, S. G., J. T. NELSON, P. HARRITY, J. KUHN, M. KUHN, C. KUEHLER, AND J. G. GIFFIN. 2001. Re-introduction and translocation of a Hawaiian solitaire: a comparison of methods. *Studies in Avian Biology* 22:347–353.
- FANCY, S. G., T. J. SNETSINGER, AND J. D. JACOBI. 1997. Translocation of the Palila, an endangered Hawaiian honeycreeper. *Pacific Conservation Biology* 3: 39–46.
- HARRITY, P., C. KUEHLER, J. KUHN, M. KUHN, AND A. LIEBERMAN. 1995. Hawaiian endangered bird conservation program: 1995 report to the U.S. Fish and Wildlife Service. The Peregrine Fund, Boise, Idaho.
- KEPLER, C. B. AND A. K. KEPLER. 1983. A first record of the nest and chicks of the Small Kaua'i Thrush. *Condor* 85:497–499.
- KUEHLER, C., A. LIEBERMAN, P. HARRITY, M. KUHN, J. KUHN, B. MCILRAITH, AND J. TURNER. 2001. Restoration techniques for Hawaiian forest birds: collection of eggs, artificial incubation and hand-rearing of chicks, and release to the wild. *Studies in Avian Biology* 22:354–358.
- KUEHLER, C., A. LIEBERMAN, P. OESTERLE, T. POWERS, M. KUHN, J. KUHN, J. T. NELSON ET AL. 2000. Development of restoration techniques for Hawaiian thrushes: collection of wild eggs, artificial incubation, hand-rearing, captive-breeding and reintroduction to the wild. *Zoo Biology* 19:263–277.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- PERKINS, R. C. L. 1903. *Vertebrata [Aves]*. Pages 368–465 in *Fauna Hawaiiensis* (D. Sharp, Ed.), vol. 1, part IV. University Press, Cambridge, United Kingdom.
- PRATT, H. D. 1982. Relationships and speciation of the Hawaiian thrushes. *Living Bird* 19:73–90.
- PRATT, T. K., S. G. FANCY, AND C. J. RALPH. 2001. Akiapolaau (*Hemignathus munroi*) and Nukupuu (*Hemignathus lucidus*). *The Birds of North America*, no. 600.
- PYLE, R. L. 1994. Hawaiian Islands region. *Field Notes* 48:251–252.
- REYNOLDS, M. H. AND T. J. SNETSINGER. 2001. The Hawaii rare bird search 1994–1996. *Studies in Avian Biology* 22:133–143.
- RICHARDSON, F. AND J. B. BOWLES. 1964. A survey of the birds of Kauai, Hawaii. B. P. Bishop Museum Bulletin, no. 227. Honolulu, Hawaii.
- SCOTT, J. M., S. MOUNTAINSPRING, F. L. RAMSEY, AND C. B. KEPLER. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. *Studies in Avian Biology* 9:1–431.
- SINCOCK, J. L., R. E. DAEHLER, T. TELFER, AND D. H. WOODSIDE. 1984. Kauai forest bird recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon.
- SNETSINGER, T. J., M. H. REYNOLDS, AND C. M. HERRMANN. 1998. Ou (*Psittirostra psittacea*) and Lanai Hookbill (*Dysmorodrepanis munroi*). *The Birds of North America*, nos. 335–336.
- SNETSINGER, T. J., K. M. WAKELEE, AND S. G. FANCY. 1999. Puaiohi (*Myadestes palmeri*). *The Birds of North America*, no. 461.
- SYKES, P. W., JR., A. K. KEPLER, C. B. KEPLER, AND J. M. SCOTT. 2000. Kauai Oo (*Moho braccatus*), Oahu Oo (*Moho apicalis*), Bishop's Oo (*Moho bishopi*), Hawaii Oo (*Moho nobilis*), and Kioea (*Chaetoptila angustipluma*). *The Birds of North America*, no. 535.
- TWEED, E. J., J. T. FOSTER, B. L. WOODWORTH, P. OESTERLE, C. KUEHLER, A. A. LIEBERMAN, A. T. POWERS ET AL. 2003. Survival, dispersal, and home-range establishment of reintroduced captive-bred Puaiohi, *Myadestes palmeri*. *Biological Conservation* 3:1–9.
- VANDERWERF, E. A. 1998. Elepaio (*Chasiempis sandwicensis*). *The Birds of North America*, no. 344.
- VEITCH, C. R. AND B. D. BELL. 1990. Eradication of introduced mammals from the islands of New Zealand. Pages 137–146 in *Ecological restoration of New Zealand islands* (D. R. Towns, C. H. Daugherty, and I. E. Atkinson, Eds.). Conservation Sciences Publication, no. 2. Department of Conservation, Wellington, New Zealand.
- WAKELEE, K. M. AND S. G. FANCY. 1999. Omao (*Myadestes obscurus*), Kamao (*Myadestes myadestinus*), Olomao (*Myadestes lanaiensis*), and Amaui (*Myadestes woahensis*). *The Birds of North America*, no. 460.